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LAKE MICHIGAN BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2021

Technical Report



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January 2023

Suggested citation for the report:

Burlakova, L. E. and Karatayev, A.Y. 2023. Lake Michigan Benthos Survey Cooperative Science and Monitoring Initiative 2021. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State University, Buffalo, NY.

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<http://greatlakescenter.buffalostate.edu/sites/greatlakescenter.buffalostate.edu/files/uploads/Documents/Publications/LakeMichiganBenthosSurveyCSMI2021FinalReport.pdf>

TECHNICAL REPORT: LAKE MICHIGAN BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2021

Lake and Year: Lake Michigan, 2021

Lead Organization: SUNY Buffalo State University

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Project Overview

In this report, we present results of a benthic survey of Lake Michigan conducted as part of the United States Environmental Protection Agency (U.S. EPA) Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP). Consistent with the sampling scheme of previous CSMI benthic surveys, a lake-wide survey was conducted in 2021 at 95 stations in Lake Michigan to assess the status of the benthic macroinvertebrate community and at an additional 19 stations sampled exclusively for *Dreissena* and Amphipoda. The project was organized around the Lake Michigan 2021 science priorities to continue nearshore to offshore monitoring of key food web components (e.g., phytoplankton, zooplankton, *Diporeia* and dreissenid mussels) that will further our understanding of the current and future impacts of aquatic invasive species upon the health of the Lake Michigan ecosystem. The primary focus of this survey was the status of benthic community, including the invasive quagga mussels (*D. rostriformis bugensis*) in comparison with historic data. In addition, we compared the results of rapid video assessment of dreissenid populations with data obtained from traditional Ponar grabs to assess the advantages and disadvantages of both methods.

Study Highlights

- 106 species and higher taxa of benthic macroinvertebrates were found in Lake Michigan in 2021. The most diverse and most widely occurred taxa throughout the lake were Oligochaeta, representing 20% of lake-wide density and 0.2% of biomass.
- *Diporeia* was found at only 10 stations (9% of total) at low densities and continues to decline even in the deepest parts of the lake. Similar continuous decline was found in densities of sphaeriids. In contrast, Oligochaeta abundance progressively increased in shallow and intermediate-depth intervals in the last decade.
- Exotic mollusc New Zealand mud snail *Potamopyrgus antipodarum*, first recorded in the lake in 2006, increased in abundance and distribution in the last 5 years. In 2021 species lake-wide density

increased 25-fold compared to 2015, comprising 93% of total lake-wide gastropod density and 79% of biomass, and its occurrence increased 3-fold.

- Exotic bivalve *Dreissena r. bugensis* was found at 98% of all stations and comprised 75% of lake-wide benthos density and 99.7% of biomass. Lake-wide quagga mussel population in 2021 exceeded 2015 density by 30% largely due to a 3-fold increase in density in the shallowest depth zone caused by recently settled mussels. A significant increase in both quagga mussel density and biomass was found only in the deepest zone (>90 m). Overall, the last 10 years lake-wide population density of quagga mussels somewhat stabilized, although there is an ongoing change in the spatial distribution with the bulk of mussel populations expanding to deep depths.
- Lake-wide *Dreissena* occurrence obtained using Benthic Imaging System (BIS) was only slightly lower than occurrence obtained using Ponar grab (94% vs. 98%). The difference between lake-wide average densities estimated using videography and Ponar for mussels >5 mm was within 10% supports our assessment that underwater videography could be a very useful tool in *Dreissena* rapid population assessment.

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CHAPTER 1. MAJOR FINDINGS FROM THE CSMI BENTHIC MACROINVERTEBRATE SURVEY IN LAKE MICHIGAN IN 2021 WITH AN EMPHASIS ON LONG-TERM TRENDS IN BENTHIC COMMUNITY

Overview

A lake-wide benthic survey of Lake Michigan was conducted in 2021 as part of the U.S. EPA Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP). Consistent with the sampling scheme of previous CSMI benthic surveys, benthic samples were collected at 95 stations to assess the status of the benthic macroinvertebrate community, and at an additional 19 stations sampled exclusively for invasive mussel *Dreissena* and deep-water amphipod *Diporeia* to follow long-term trends in their distribution.

Lake Michigan has one of the longest time series (spanning almost a century) of benthic surveys in the Laurentian Great Lakes (Mehler et al., 2020). One of the first larger scale benthic studies conducted in 1893 in the Traverse Bay region found that the benthic community was dominated by *Pontoporeia hoyi* (currently *Diporeia*) (Ward, 1896). *Diporeia* remained the dominant species in 1931 and 1932 (Eggleton, 1937) and together with Oligochaeta and Sphaeriidae they comprised about 94% of benthic species abundance in Lake Michigan. In 1964-67, Alley and Mozley (1975) found a similar pattern in the benthic community, but densities of *Diporeia*, Oligochaeta, and Sphaeriidae in the 1960s were 1.5, 2.6, and 4.3 times higher compared to those of 1931, likely due the significant increase in plankton standing crop between the late 1920s and late 1950s (Damann, 1960). Continued increases in the abundances of *Diporeia*, Oligochaeta, and Sphaeriidae in nearshore waters in the 1970s and early 1980s were attributed to increasing nutrient loads and greater lake productivity (Madenjian et al., 2002; Nalepa, 1987). During the 1980s and early 1990s, since the implementation of the Great Lakes Water Quality Agreement, primary production in the nearshore waters declined (Johengen et al., 1994, Madenjian et al., 2002), likely causing a decline in abundances of *Diporeia*, Oligochaeta, and Sphaeriidae (Madenjian et al., 2002; Nalepa et al., 1998). The introduction of *D. polymorpha* (in 1989, Griffiths et al., 1991) and *D. r. bugensis* (1997, Nalepa et al., 2001) and expansion of *D. r. bugensis* to deeper depths in the 2000s were associated with a further decline in primary production (Madenjian et al., 2015) and a general shift in production from the pelagic to the benthic zone (Cuhel & Aguilar 2013), followed by the drastic lake-wide decline of *Diporeia* (Nalepa et al., 2009).

The objective of this study was to describe the status of Lake Michigan benthic community, including the invasive zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*) in comparison with historic data. This report contains detailed descriptions of benthic communities in Lake Michigan in 2021, including information on sampling design (station locations, sampling and laboratory procedures), the taxonomy and abundance of benthic invertebrates, and long-term changes in major taxonomic groups since the 1930s. Detailed analysis of results obtained within this study are being prepared for peer-reviewed publications.

Methods

Sampling protocol

Samples for benthic macroinvertebrates were collected in triplicate from 99 CSMI stations located throughout Lake Michigan in July 13-22, 2021 (Fig. 1.1, Appendix), including historically sampled sites. Of

Laboratory Procedures

All organisms found in each replicate sample collected at the 95 benthos stations were sorted, identified, counted, and weighed (total wet weight). Organisms were separated under low magnification using a dissecting microscope. Oligochaetes and chironomids were mounted on slides and identified using a compound microscope; other organisms were identified using a dissecting microscope. Adult oligochaetes and Naididae were identified to species; immature Tubificidae, Lumbriculidae, and Enchytraeidae were identified to the lowest taxonomic level possible, usually family, and included in density and biomass estimates. Counts of oligochaete fragments were excluded from density analyses but fragment weight was considered in the determination of biomass. Immature Oligochaeta (in cocoons) were recorded but excluded both from density and biomass calculations for comparison with historic data. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible.

Dreissena from all samples were identified to species, measured to the nearest millimeter with a caliper, counted, and the whole sample was weighed to the nearest 0.0001 g after being blotted dry on absorbent paper (total wet weight of tissue and shell, TWW); details are described in the EPA GLNPO Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (US EPA, 2015: SOP LG407, Revision 09, April 2015). All *Dreissena* collected during this survey were quagga mussels (*D. rostriformis bugensis*).

Historic data

Historic data sets, spanning between 1931/32 and 2015 (Eggleton, 1937; Alley & Mozley, 1975; Nalepa et al., 2014; Karatayev & Burlakova, 2017; Nalepa et al., 2017; Mehler et al., 2020) were used to examine long-term changes in major benthic taxonomic groups in Lake Michigan (details in Mehler et al., 2020). The long-term data included only stations from the main basin (e.g., excluding Green Bay, Thunder Bay, and Muskegon Bay), and used ash free dry tissue weight (AFDTW) of *Dreissena*.

Data analysis

To test for differences in benthic community composition between time periods and between depth zones, Analysis of Similarity (ANOSIM) was used in Primer 7 (Plymouth Routines in Multivariate Ecological Research, Version 7.0.13, Primer E- Ltd. 2006) performed on Bray-Curtis similarity matrix calculated on fourth-root transformed benthic densities. Differences in benthic community composition between lake regions and depth zones were considered significant when $P < 0.05$, and the test statistic R was used as an index of the degree of separation between groups. Similarity Percentage (SIMPER) analysis was used to determine the contribution of species to similarity among depth zones. We used shade (“heat map”) plots presenting the species clustered against sampled stations to provide a visual representation of the data matrix. The species Y axis is re-ordered in line with a cluster analysis of the species, using Whittaker’s Index of Association to give among-species similarities, and the second X-axis re-orders samples in line with a cluster analysis of the samples. Only the 30 most abundant species were used in the analysis, as inclusion of rare species cannot produce sensible assessments of similarity with other species due to their random nature of occurrences.

Results and Discussion

Status of Lake Michigan benthic community in 2021

We found 106 species and higher taxa of benthic macroinvertebrates in Lake Michigan in 2021, in addition to unidentified immature tubificids and Chironomidae. The most diverse were Oligochaeta (44 species and higher taxa), Insecta (Chironomidae, 33), Mollusca (13 species, 10 Gastropoda and 3 Bivalvia); and Malacostraca (5 species: 4 Amphipoda and 1 Mysida). Other classes were represented by less than 3 taxa, or were not identified to species level (e.g., Trichoptera, Hydrozoa, Nemertea). Among Oligochaeta, the most diverse were Tubificidae (23 species and higher taxa), and Naididae (19).

The most widely occurred taxa throughout the lake were Oligochaeta found at all 95 stations (Lumbriculidae: 88%, Tubificidae: 70%, Enchytraeidae: 50%, and tubificid *Limnodrilus hoffmeisteri*: 46%), followed by chironomids (78%, *Heterotrissocladius subpilosus* group and *Micropsectra* sp.: 43% each, *Paracladopelma winnelli*: 27%). Exotic bivalve *Dreissena r. bugensis* was found at 98% of all 114 stations sampled for benthos and *Dreissena*.

Another exotic mollusc, gastropod *Potamopyrgus antipodarum*, was first recorded in the lake in 2006 (Benson et al., 2022) and during 2015 CSMI survey was found at 9 stations (7% of total) at average lake-wide densities 3.1m^{-2} and biomass 0.03 gm^{-2} . In 2021 *P. antipodarum* was found at average densities of 78 m^{-2} and biomass 0.31 gm^{-2} at 21% of stations, comprising 93% of total lake-wide gastropod density and 79% of biomass. *Diporeia* was found at low abundance (average density 12.4 m^{-2} , average biomass 0.013 gm^{-2}) only at 10 of all 114 benthic and “*Dreissena* and Amphipoda” stations combined. *Mysis* was recorded at low density at 36% (34) of all stations (Table 1.1).

Dreissena r. bugensis comprised a large percentage of lake-wide benthos density (75%), followed by Oligochaeta (20%), Chironomidae (3%) and non-dreissenid Mollusca (1.2%). Contribution of other groups (Amphipoda, Hirudinea, Trichoptera, Platyhelminthes, etc.) to total benthos density was less than 1% each. Among Oligochaeta, the most numerous were Tubificidae (65%) and Lumbriculidae (28%).

Dreissena r. bugensis dominated lake-wide benthos by biomass (99.7% of total wet biomass, Table 1.1). The remaining benthic biomass was represented by Oligochaeta (0.21%, dominated by Lumbriculidae (50%) and Tubificidae (23%)), Mollusca (other than *Dreissena*, 0.04%; mainly *P. antipodarum*, 0.03%), and Chironomidae (0.01%) (Table 1.1).

Benthic communities were not different between central and northern ($R = 0.03$, $P = 0.10$), central and southern ($R = 0.01$, $P = 0.24$), and northern and southern regions ($R = 0.10$, $P = 0.015$) (Fig. 1.2A). Only communities in Green Bay were significantly different from all other regions ($P < 0.02$, pairwise tests after 1-way ANOSIM), likely due to their location in shallow depths: benthic communities were significantly different among depth zones ($R = 0.57$, $P = 0.01$, 1-way ANOSIM, Fig. 1.2B), and the largest differences were found between 0-30 and >50 m ($R > 0.60$, $P < 0.01$).

Dreissena r. bugensis, Lumbriculidae (both immature and mature *Stylodrilus heringianus*) and Chironomidae *Heterotrissocladius subpilosus* group were the most contributing species (>87% combined) to similarity of communities at depths >50 m (SIMPER, Fig. 1.3, note the cluster of species in Fig. 1.4).

Shallow benthic communities (<30 m) were more diverse but still characterized mainly by *D. r. bugensis* and tubificids.

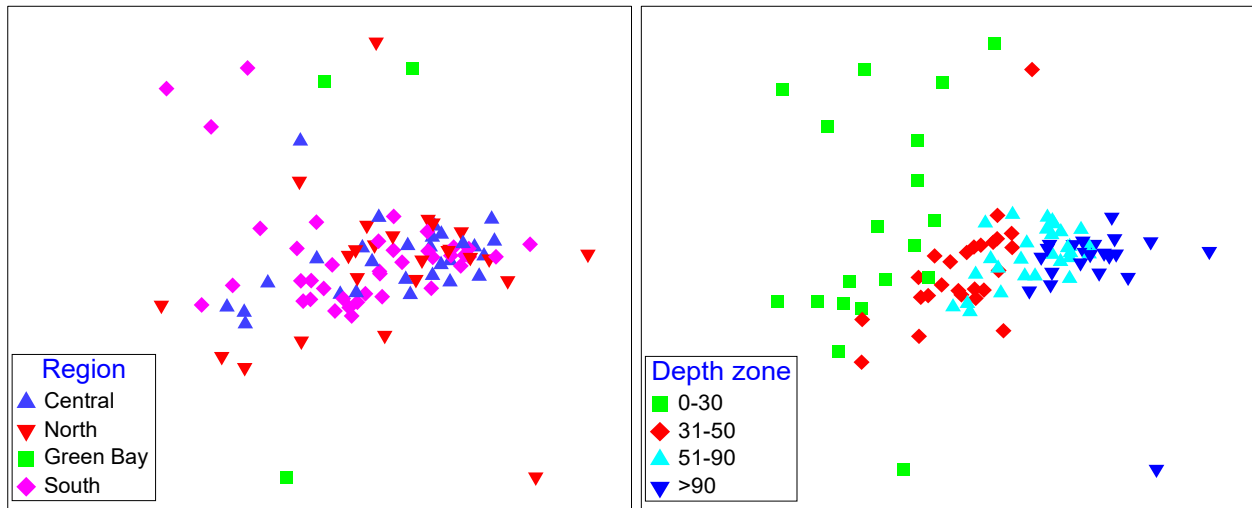


Figure 1.2. Non-parametric multidimensional (NMDS) ordination plots of Lake Michigan benthic community structure in 2021 (Stress = 0.16). Density (ind./m²) of benthic taxa collected at all permanent sites were fourth-root transformed and converted to similarity matrix using Bray-Curtis similarity index. Stations are indicated by: A) lake regions (blue triangles – central, red inverse triangles – northern, green squares – Green Bay, magenta diamonds – southern Lake Michigan) and B) by depth zones (green squares – 0-30 m, red diamonds – >30-50 m, blue triangles – >50-90 m, dark blue inverse triangles – >90 m). The largest differences were found among the shallow (0-30 m) and deeper lake zones, while communities were not well separated by lake region.

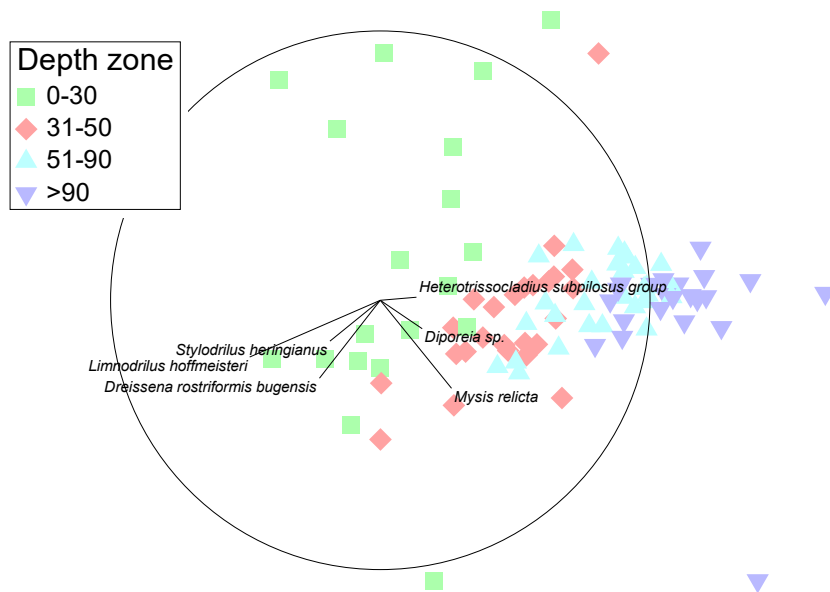


Figure 1.3. Non-parametric multidimensional (NMDS) ordination plots of Lake Michigan benthic community structure in 2021 (Stress = 0.16). Stations are indicated by depth zones (green squares – 0-30 m, red diamonds – >30-50 m, blue triangles – >50-90 m, dark blue inverse triangles – >90 m). Species that have the largest correlations with NMDS 1 and 2 and responsible for the differences among the depth zones are indicated.

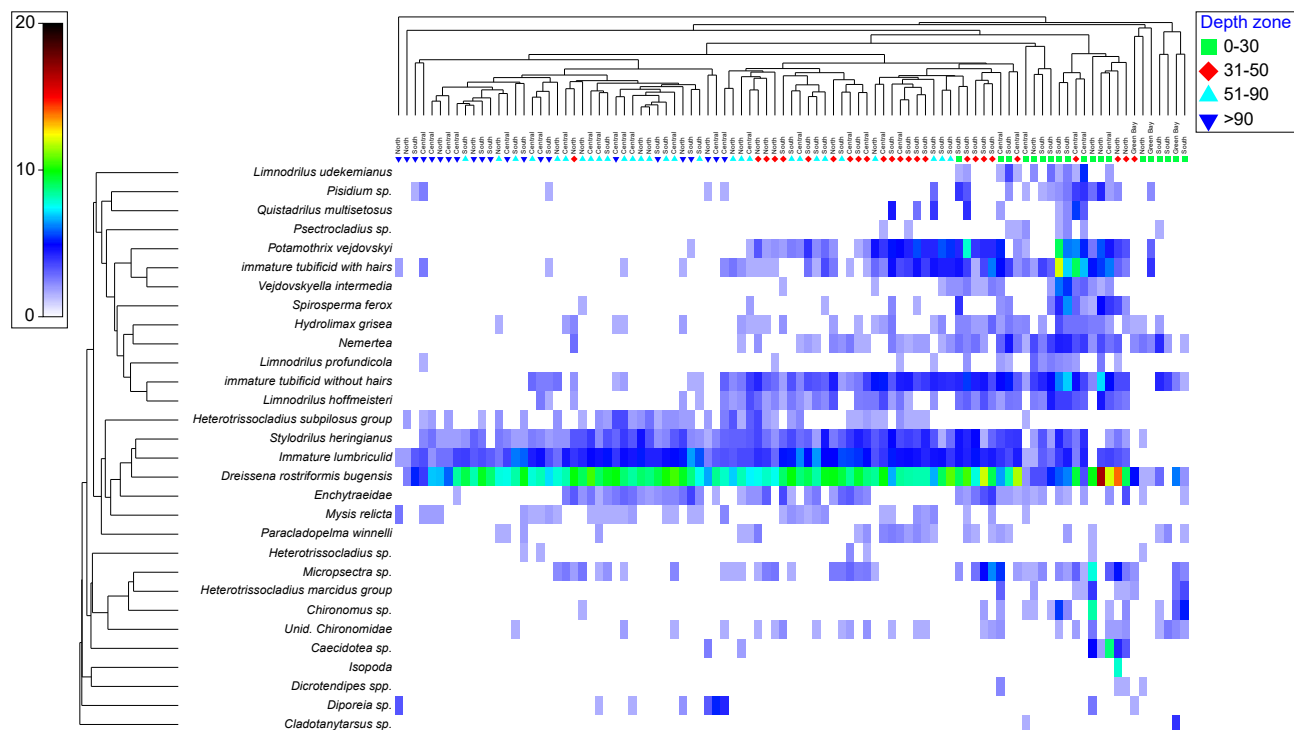


Figure 1.4. Shade plot grouping of benthic species and Lake Michigan stations where they were collected in 2021. Color intensity increases with species density; station and species clustering categories are indicated in the legends. The Y axis is ordered in line with a cluster analysis of the species (using Whittaker’s Index of Association). Only 30 most abundant species were used in the analysis. Note the *Dreissena*-associated cluster of species at deep stations.

Table 1.1. Average (\pm standard error) density (ind. m^{-2}) and wet biomass (g m^{-2}) of major taxonomic groups of benthic invertebrates collected from 95 benthic stations in Lake Michigan in 2021 and averaged by depth zones, and lake-wide average (not stratified by depth). n.r. – not recorded. Number of stations given in parentheses. Average densities and biomass of *Diporeia* and *Dreissena* are provided separately for the benthic survey (95 stations), and for all sampled stations (e.g., combined 95 benthic stations and additional 19 “*Dreissena* and *Diporeia* only” stations, total 114 stations*).

Taxa	0 – 30 m (19)	>30 – 50 m (25)	>50 – 90 m (29)	>90 m (22)	Lake-wide (95)
Amphipoda** (ind. m^{-2})	1.3 \pm 0.8	0.26 \pm 0.26	0.22 \pm 0.22	n.r.	0.40 \pm 0.19
Amphipoda** (g m^{-2})	<0.001	<0.001	<0.01	n.r.	<0.001
Chironomidae (ind. m^{-2})	750 \pm 523	221 \pm 71	40 \pm 9	17 \pm 7	224 \pm 108
Chironomidae (g m^{-2})	0.34 \pm 0.26	0.12 \pm 0.03	0.04 \pm 0.01	0.02 \pm 0.01	0.11 \pm 0.05
<i>Diporeia</i> (95 stations)					
(ind. m^{-2})	2.7 \pm 2.7	0.3 \pm 0.3	0.4 \pm 0.3**	59.1 \pm 35.9	14.4 \pm 8.5**
<i>Diporeia</i> (95 stations)					
(g m^{-2})	0.004 \pm 0.004	0.001 \pm 0.001	0.003 \pm 0.003**	0.054 \pm 0.027	0.014 \pm 0.007**
<i>Diporeia</i> (114 stations)					
(ind. m^{-2})	2.3 \pm 2.3	0.2 \pm 0.2	1.5 \pm 1.2	59.1 \pm 35.9	12.4 \pm 7.2

Taxa	0 – 30 m (19)	>30 – 50 m (25)	>50 – 90 m (29)	>90 m (22)	Lake-wide (95)
<i>Diporeia</i> (114 stations)					
(g m ⁻²)	0.003±0.003	0.001±0.001	0.008±0.006	0.054±0.027	0.014±0.006
<i>Dreissena</i> (95 stations)					
(ind. m ⁻²)	6581±4075	8199±1510	6329±559	4181±648	6374±927
<i>Dreissena</i> (95 stations)					
(g m ⁻²)	447±282	1432±199	1257±78	538±108	975±94
<i>Dreissena</i> (114 stations)					
(ind. m ⁻²)	6587±3544	7650±1212	6676±471	4181±648	6451±785
<i>Dreissena</i> (114 stations)					
(g m ⁻²)	430±243	1380±162	1256±69	538±108	993±81
Sphaeriidae (ind. m ⁻²)	54±23	14±9	2±2	3±2	16±6
Sphaeriidae (g m ⁻²)	0.1±0.4	0.01±0.04	0.03±0.03	0.004±0.003	0.03±0.01
Gastropoda (ind. m ⁻²)	377±298	31±13	2±1	n.r.	84±60
Gastropoda (g m ⁻²)	1.5±1.2	0.4±0.2	<0.01	n.r.	0.4±0.2
<i>Mysis</i> (ind. m ⁻²)	0.3±0.3	3.1±1.0	5.5±1.3	7.5±2.7	4.3±0.8
<i>Mysis</i> (g m ⁻²)	0.001±0.001	0.05±0.02	0.05±0.01	0.10±0.05	0.05±0.01
All Oligochaeta (ind. m ⁻²)	3903±1828	1964±450	955±117	351±100	1670±400
All Oligochaeta (g m ⁻²)	2.44±0.70	2.93±0.43	1.91±0.26	0.79±0.22	2.03±0.22
-Lumbriculidae (ind. m ⁻²)	212±62	577±73	653±81	318±92	467±43
-Lumbriculidae (g m ⁻²)	0.52±0.17	1.46±0.25	1.26±0.18	0.57±0.16	1.01±0.11
-Naididae (ind. m ⁻²)	392±148	78±24	11±4	n.r.	102±33
-Naididae (g m ⁻²)	0.04±0.02	0.008±0.002	0.002±0.001	n.r.	0.011±0.004
-Tubificidae (ind. m ⁻²)	3292±1676	1265±448	273±99	19±9	1079±371
-Tubificidae (g m ⁻²)	1.24±0.37	0.59±0.19	0.15±0.05	0.03±0.02	0.46±0.10
All benthos (ind. m ⁻²)	12186±4998	10654±1759	7340±587	4621±705	8552±1142
All benthos (g m ⁻²)	452±283	1436±199	1259±78	539±108	978±94
All benthos					
w/o <i>Dreissena</i> (ind. m ⁻²)	5604±2027	2455±506	1011±117	440±103	2177±462
All benthos					
w/o <i>Dreissena</i> (g m ⁻²)	4.73±1.60	3.53±0.48	2.04±0.27	0.97±0.22	2.75±0.38

* The distribution of all 114 stations by depth zones (together with the 19 *Dreissena* and *Diporeia*-only stations) was: 0 – 30 m (22 stations); >30 – 50 m (32); >50 – 90 m (38); and >90 m (22), total 114 stations.

**other than *Diporeia*

Long-term trends in benthos

Since 2021 was only the second (after 2015) survey when the entire benthic community was examined, lake-wide long-term trends in taxa other than *Diporeia*, Oligochaeta and Sphaeriidae could not be assessed. 2021 survey data show that the amphipod *Diporeia* continued to decline (Table 1.2, Fig. 1.5). In 2015, *Diporeia* was collected at only one station that was < 90 m, and at 9 stations that were >90 m. In comparison, in 2021 *Diporeia* was collected at 5 stations <90 m (including one shallow station in northern region at 24 m depth, and another one in Green Bay at 44 m depth), and at 5 stations >90 m. While at depths <90 m *Diporeia* densities were extremely low and did not change, in the deepest zone (>90) we

found an almost 9-fold decline compared to 2015 (Table 1.2) along with the total bottom area occupied by *Diporeia* (Fig. 1.5).

Diporeia was historically the most abundant benthic macroinvertebrate in the lake contributing >65% to the total benthic density in the 1930s at depths <50 m (Eggleton, 1937). *Diporeia*, Oligochaeta, and Sphaeriidae experienced an increase in abundance in nearshore waters (<50 m) during 1964–1980 (Table 1.2), when P loading was presumably increasing, and declined in the nearshore in the next decade when P loading was decreasing (Mehler et al., 2020). The drastic decrease in *Diporeia* abundance in the late 1980s and in the 2010s has been attributed to the decline in primary production and indirect impacts of the dreissenid mussel invasions (Madenjian et al., 2015; Nalepa et al., 1998; Mehler et al., 2020). Our study indicated that this decline in *Diporeia* is ongoing even in the deepest part of the lake.

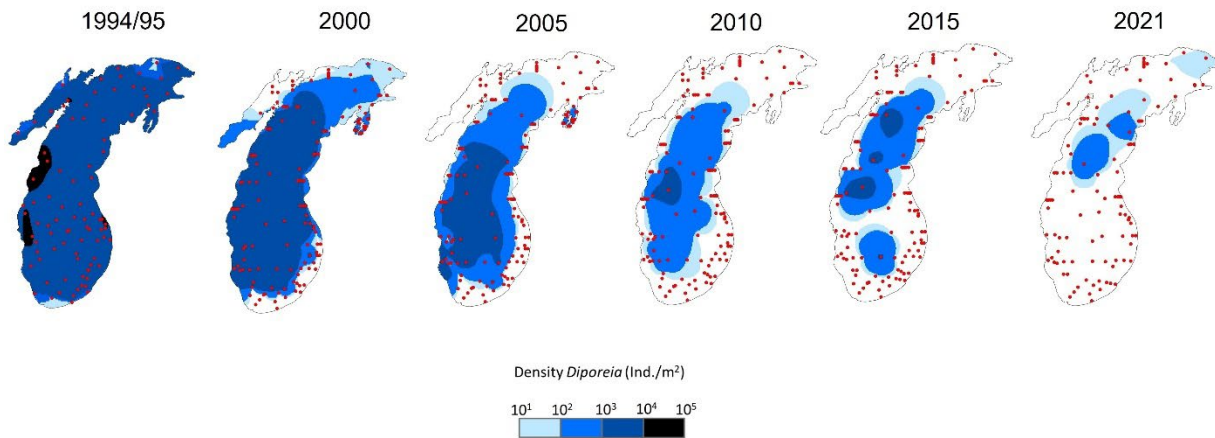


Figure 1.5. Spatial distribution of *Diporeia* sp. in Lake Michigan from 1994 to 2021, expressed as density (ind.m⁻²). Red dots indicate sampling stations.

Similar continuous decline was found in densities of sphaeriids that were lower at all depth intervals in 2015 and 2021 compared to the 1960s (Table 1.2). A decline in sphaeriids at all depths was first observed soon after *Dreissena* became established in the southern basin (Nalepa et al., 1998), likely due to competition with *Dreissena* for available food.

Oligochaeta abundance somewhat increased in the last decade indicating that dreissenids may have positive effects on Oligochaeta abundance (Mehler et al., 2020; Bayba et al., 2022; Table 1.2). *Dreissena* filters particulate material (mainly phytoplankton) from the water column and subsequently deposits this organic material in the benthic zone in the form of feces and pseudofeces. This fresh organic material is quickly utilized by bacteria (Lohner et al., 2007), and both serve as an added food source for benthic detritivores (MacLellan-Hurd, 2020; Eifert et al., in review). Oligochaetes are detritivores and thus likely benefit from these added food inputs.

Table 1.2. Dynamics of mean (+ standard error) densities of major benthic macroinvertebrate taxa in Lake Michigan from 1930 to 2021 by depth zones. Density data for 1931/32 are from Eggleton (1937) and Mehler et al. (2020); for 1964–67 are from Alley & Mozley (1975); for 1994/95, 2000, 2005, and 2010 are from Nalepa et al. (2014); and 2015 and 2021 from Karatayev & Burlakova (2017), Nalepa et al. (2017), this report. n/d – taxa not documented.

Depth zone	Taxa/Year	1931/32	1964-67	1994/95	2000	2005	2010	2015	2021
<30m	<i>Diporeia</i>	716±218	4945±1160	3907±1005	853±315	104±88	1±1	0	2.7±2.7
	Oligochaeta	174±48	2152±927	n/d	n/d	n/d	n/d	2985±726	3903±1828
	Sphaeriidae	73±19	1357±505	n/d	n/d	n/d	n/d	76±36	54±23
>30-50 m	<i>Diporeia</i>	1387±293	7559±829	6111±1377	2116±563	24±16	<1	0	0.3±0.3
	Oligochaeta	352±139	2469±718	n/d	n/d	n/d	n/d	3568±603	1964±450
	Sphaeriidae	211±70	3022±552	n/d	n/d	n/d	n/d	5±6	14±9
>50-90 m	<i>Diporeia</i>	875±114	3976±454	6521±562	3469±464	548±131	98±49	0.2±0.2	1.9±1.5
	Oligochaeta	312±60	1181±440	n/d	n/d	n/d	n/d	1625±253	955±117
	Sphaeriidae	108±24	1015±370	n/d	n/d	n/d	n/d	2±1	2±2
>90 m	<i>Diporeia</i>	557±77	2065±331	4547±385	2804±453	1244±217	429±122	528±186	59±36
	Oligochaeta	192±46	387±81	n/d	n/d	n/d	n/d	558±96	351±100
	Sphaeriidae	16±5	124±39	n/d	n/d	n/d	n/d	18±4	3±2

***Dreissena* spatial and temporal trends**

Long-term dynamics in zebra and especially quagga mussels in Lake Michigan are well documented (Karatayev et al., 2021a; Mehler et al., 2020; Nalepa et al., 2017, 2020). Below is a brief analysis of changes in *Dreissena* spp. population in 2021 compared to the previous years. For consistency with long-term data, for this analysis we excluded Green Bay data and used ash free dry tissue weight (AFDTW, calculated from total wet weight (TWW) using Nalepa et al. (2018) relationship $gAFDTW = 0.01996 * gTWW$).

Previous studies in Lake Michigan have shown that dreissenids reached their population maximum in the shallow (0-30 m) to mid (>30-50 m and >50-90 m) depth zones by 2010, 13 years after the first detection in the lake in 1997, and then declined (Fig. 1.6, 1.7; Karatayev et al., 2021a; Mehler et al., 2020; Nalepa et al., 2017, 2020). Such a decline may be expected if quagga mussels in shallow to mid-depth zones had increased to densities greater than their carrying capacity. Similar declines in dreissenid densities in the nearshore zone, along with a shift of the maximum density to deeper areas, were also observed in lakes Huron and Ontario (Karatayev et al., 2020, 2021a, 2021b, 2022). In the deepest zone (>90 m) mussel population was always growing. The increases in mussel density at depths >90 m have a strong influence on lake-wide values because by area, 43.5% of the lake bottom is >90 m deep.

Data from our previous survey conducted in 2015 demonstrated that the lake-wide population of dreissenids declined for the first time since their invasion (Fig. 1.7, Table 1.3). This decline potentially indicated that the lake-wide population of quagga mussels in Lake Michigan might have reached its carrying capacity, and further decline could be expected in 2021. In contrast to our predictions, lake-wide quagga mussel population in 2021 exceeded 2015 density by 30%. This increase, however, was not significant lake-wide due to a large variation in mussel densities across depth zones ($P = 0.372$, Kruskal-Wallis test).

Even more unexpected was an over 3-fold increase in mussel density in the shallowest depth zone, caused mostly by large densities of small (<5 mm) recently settled mussels comprising 87% of all dreissenids in this zone. This increase, however, was again not significant due to large variability in densities at these shallow depths ($P = 0.66$, Fig. 1.7). As survival of small mussels over winter is low, further observations are needed to evaluate whether this increase will transform into an increase in densities in this shallowest zone long-term. As expected, there was a further increase (by 60%) in quagga mussel density in the deepest zone (>90 m), and this increase was significant ($P = 0.031$, multiple comparisons after Kruskal-Wallis test). Changes in quagga mussel biomass in 2021 compared to 2015 were smaller than in density and a significant increase was found at the >90 m zone only ($P = 0.041$). The lake-wide (excluding Green Bay) AFDTW biomass did not change significantly ($P = 0.61$). Overall, recent data suggest that during the last 10 years (since 2010) lake-wide population density of quagga mussel in Lake Michigan has stabilized, although there is an ongoing change in the spatial distribution with the bulk of mussel populations expanding to deep depths (Fig. 1.6, 1.7). Similar patterns were recorded in other deep Great Lakes (Karatayev et al., 2020, 2021a, 2021b, 2022; Karatayev & Burlakova, 2022).

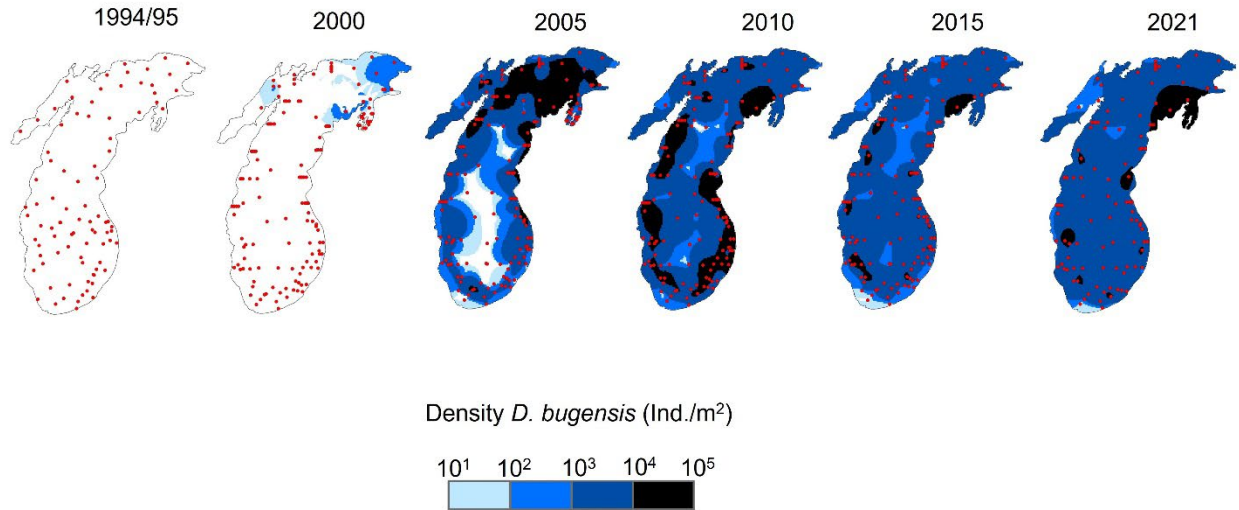


Figure 1.6. Spatial distribution of *Dreissena rostriformis bugensis* in Lake Michigan from 1994 to 2021, expressed as density (ind.m⁻²). Red dots indicate sampling stations.

Table 1.3. Long-term dynamics of *Dreissena polymorpha* and *D. rostriformis bugensis* density (m⁻²) in Lake Michigan (excluding Green Bay). Average ± standard errors. Here lake-wide densities were calculated as weighted averages from four depth zones. Sample size given in parenthesis.

Depth / Species	1994 (84)	2000 (129)	2005 (145)	2010 (150)	2015 (149)	2021 (111)
0-30 m						
<i>D. polymorpha</i>	730±510	1827±467	261±90	0	0	0
<i>D. r. bugensis</i>	0	37±23	6412±1418	9443±1594	2405±710	7175±3382
Both species	730±510	1864±470	6673±1456	9443±1594	2405±710	7175±3382
>30-50 m						
<i>D. polymorpha</i>	231±219	1316±570	385±98	0.5±0.5	0	0
<i>D. r. bugensis</i>	0	25±17	16213±2583	13572±1424	6105±633	7876±1230
Both species	231±219	1340±585	16598±2601	13573±1423	6105±633	7876±1230
>50-90 m						
<i>D. polymorpha</i>	0.2±0.2	16±8	34±27	0	0	0
<i>D. r. bugensis</i>	0	0	6382±1559	14555±1220	8977±745	6676±471
Both species	0.2±0.2	16±8	6416±1573	14555±1220	8977±745	6676±471
>90 m						
<i>D. polymorpha</i>	0	0	0	0	0	0
<i>D. r. bugensis</i>	0	0	749±740	2346±890	2598±718	4181±648
Both species	0	0	749±740	2346±890	2598±718	4181±648
Lake-wide						
<i>D. polymorpha</i>	188±116	550±120	107±24	0	0	0
<i>D. r. bugensis</i>	0	11±6	4958±643	7991±619	4428±398	5826±933
Both species	188±116	561±122	5065±649	7991±619	4428±398	5826±933

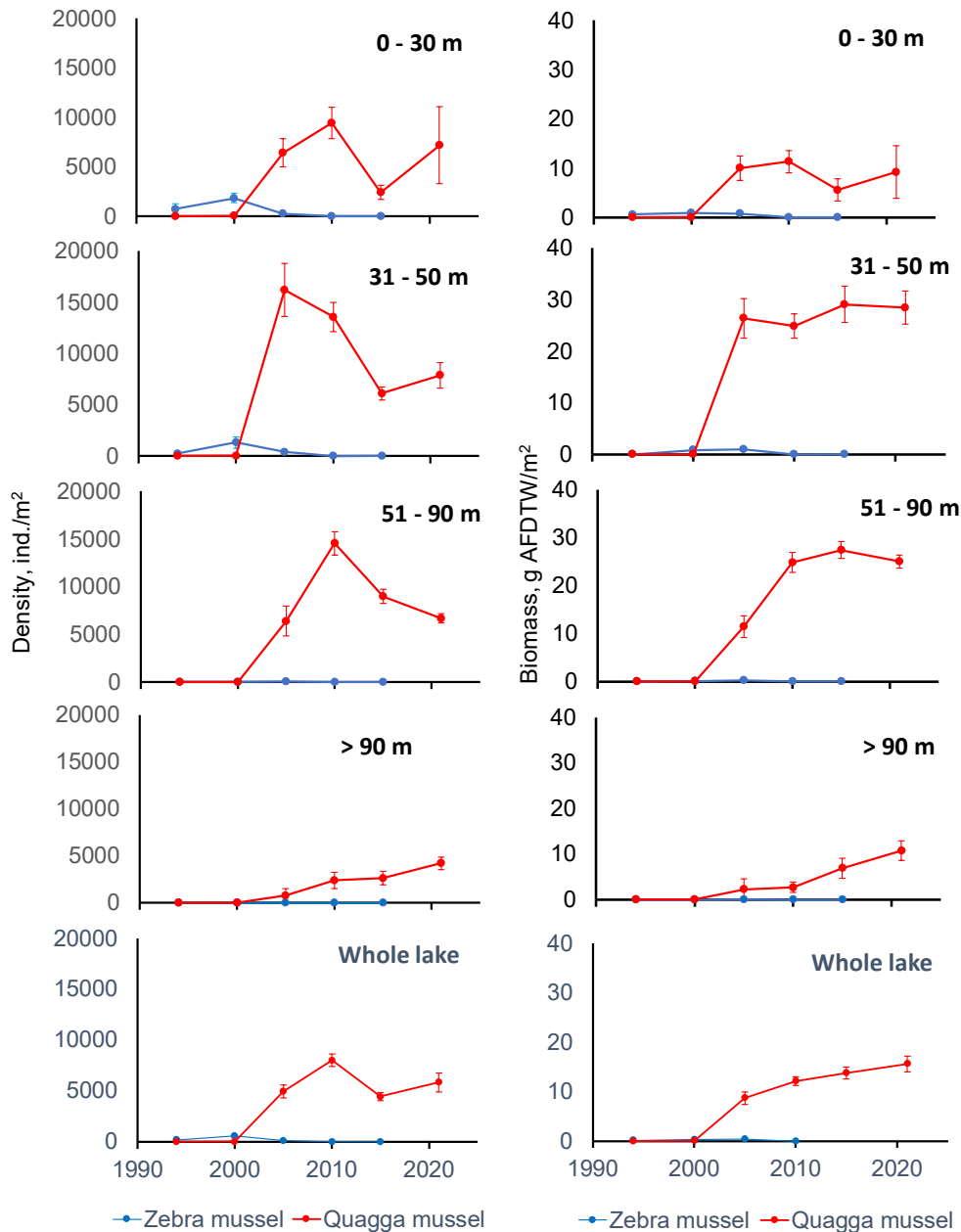


Figure 1.7. Population dynamics of quagga mussels (densities, m^{-2} and biomass, re-calculated as g of ash free dry tissue weight per m^{-2}) at different depth zones in the main basin of Lake Michigan (excluding Green Bay, Thunder Bay, and Muskegon Bay). Vertical lines denote standard error of mean. Whole lake densities and biomass are represented by means stratified by depth zones.

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CHAPTER 2. RAPID ASSESSMENT OF *DREISSENA* POPULATIONS IN LAKE MICHIGAN USING UNDERWATER VIDEOGRAPHY

Overview

To quantify their ecological role, timely and reliable estimates of *Dreissena* densities are extremely important, however samples obtained using conventional methods (bottom grabs or diver assessments) require a long time for processing (reviewed in Karatayev et al., 2018a). Typically, results of lake-wide *Dreissena* population assessments became available for stakeholders after the sampling event in 2 years (Nalepa et al., 2010), 3 years (Hunter & Simons, 2004; Patterson et al., 2005; Karatayev et al., 2014), or even 4 years later (Watkins et al., 2007; Karatayev et al., 2018b). Underwater videography could be a useful tool providing quicker *Dreissena* population assessment (reviewed in Karatayev et al., 2018a; 2021a). Since 2015, in support of the CSMI, the Great Lakes Center at SUNY Buffalo State began conducting lake-wide *Dreissena* population assessments in the Great Lakes, based on the estimation of mussel coverage from 100 still images randomly distributed along the 500 m video footage from a GoPro camera mounted on a benthic sled towed by the U.S. Environmental Protection Agency (US EPA) R/V *Lake Guardian* (Karatayev et al., 2018a; 2020), and ground-truthed with Ponar samples. This method greatly increases the number of replicates analyzed per station and reduces the cost and time for information processing and data reporting. However, the video method does not allow for direct counting of *Dreissena* mussels and therefore a substantial amount of time is still required for Ponar sample processing (on the order of months after the sampling event) and mussel enumeration. To overcome these shortcomings, Karatayev et al. (2021a) applied a novel sampling method in 2019 by using Benthic Imaging System (BIS, a drop frame equipped with a GoPro camera) across all three Lake Erie basins to estimate *Dreissena* populations. In this study, we used the BIS across Lake Michigan to estimate *Dreissena* populations (presence/absence, and density) in near real-time (aboard R/V *Lake Guardian* during CSMI and summer cruises). These preliminary data were later compared with dreissenid data obtained from traditional Ponar grabs to assess the advantages and disadvantages of both methods.

Methods

Video images were collected during the 2021 CSMI Lake Michigan benthos survey from July 13-22 from 98 stations and during long-term monitoring sampling from September 4-9 from 16 stations using a BIS equipped with two GoPro cameras (one down-looking and one oblique (i.e., side-looking) camera), and two underwater lights per camera attached to a custom-built stainless-steel carriage. On the base of this frame is a marked scale. The down-looking camera was fixed 56 cm above substrate, and the side-looking camera was fixed 30 cm above substrate at an angle of about 45 degrees, resulting in a horizontal distance from the lens to the substrate of 1 m. At each station, the BIS was lowered from the starboard side of R/V *Lake Guardian* down to the lake bottom (US EPA, 2015, SOP LG407). The BIS remained on the lake bottom for one minute (the first replicate, or RFS). This time duration was enough to increase the probability that a clear view of the area within the marked scale would be obtained, as any resuspended sediment was allowed to settle or clear from view. After one minute, the BIS was lifted 1 to 2 m from the bottom for 30 seconds, then lowered again to remain on the lake bottom for another minute (second replicate - FD1), lifted again for 30 seconds and then lowered to remain on the lake bottom for another minute (third replicate - FD2). All replicate BIS and Ponar grab samples were collected within the boundaries of an EPA

station, with only one GPS record for each station. An EPA station is defined as a bottom area of approximately 300 m in diameter (US EPA, 2014, SOP LG100). After the frame was retrieved from the water, videos from both cameras were immediately downloaded to an external hard drive for onboard analysis. A total of 342 images from 115 stations were initially collected from the down-looking camera. At three stations, the lake bottom in all three replicates were completely covered with algae, preventing mussel counts. At four additional stations, all images were not usable due to technical problems. Of the remaining 108 stations a total of 299 usable videos were collected with at least one usable image per station. In addition, on several stations at least one replicate was excluded due to missing image (4 images, accidentally deleted), algae cover (2 images), or technical problems (15 images). Of all usable images collected, 172 were evaluated as high quality where mussels were counted with “high confidence”, 43 images as medium quality (“medium confidence”), and 56 images as low quality (“low confidence”). Twenty-eight images did not have mussels.

For each replicate, we used the clearest still image (screen shot) to estimate *Dreissena* coverage and density. Occasionally, the frame sunk into the sediment; to avoid erroneous estimation of *Dreissena* size and counts we used the screen shot taken the moment the frame hit the lakebed. For density estimations all visible mussels were counted in the entire original clipped still image and the counts were converted to density (individuals/m²) using BIS sampling area that was determined for each sample separately. For each station we averaged *Dreissena* density using all useable replicates collected at the station.

According to US EPA Standard Operation Procedure (US EPA, 2021, SOP LG410) at least 10% of randomly selected still images should be recounted by a different analyst. For this study, a *Dreissena* count error of <10% difference in density between analysis was deemed acceptable. However, a higher percentage of error was found in images with few (<30) mussels (samples 9570 RFS, 29%, and H18 FD2, 23%), or where mussels were covered with algae or mud (sample 84450 FD1, 15%). On average across all images, the difference in *Dreissena* density calculated by different analysts was 5.4%.

Results and discussion

In 2021 *Dreissena* on BIS images was found at 94% of all 107 stations sampled, with the lowest occurrences (77%) recorded in the shallowest (≤30 m) depth zone. Lake-wide occurrence obtained using BIS was only slightly lower than the percentage determined based on Ponar data (98%).

According to our rapid assessment, the average *Dreissena* densities in 2021 compared to 2015 may have declined in all depth zones except at >90 m (Table 2.1). The largest decline observed occurred in the shallowest zone, where densities decreased by a factor of 9.2, and the densities lake-wide declined by a factor of 1.4. We suggested that this decline could be due to the underestimation of small (<5 mm) mussels on video images. However, it was also possible that the *Dreissena* population in Lake Michigan continued to decline, as the average density in 2015 was 1.8-fold lower than in 2010 (Nalepa et al., 2017).

Table 2.1. *Dreissena* population density (mussels per m⁻², average ± standard error) in four depth zones and lake-wide averages (weighted by depth zone) estimated using Ponar grab in 2010 and 2015, and BIS in 2021.

Depth zone	Ponar density 2010	Ponar density 2015	BIS density 2021	Ratio between Ponar 2015 and BIS 2021
0-30	9443±1593	2404±710	259±103	9.2
>30-50	13573±1423	6105±633	3700±622	1.7
>50-90	14555±1220	8977±745	4969±330	1.8
>90	2346±890	2598±718	2581±596	1.0
Lake-wide	7991±751	4428±398	3310±283	1.4

However, when 2021 Ponar data became available, we found that, in contrast to our prediction, *Dreissena* lake-wide density have increased by 32% compared to Ponar estimates in 2015, and the largest increase (by a factor of 3) was found in the shallowest zone (Tables 2.1 and 2.2).

Comparison of BIS and Ponar data for 2021 revealed that mussel counting on video images underestimated lake-wide density by a factor of 2 (Table 2.2). The largest difference was found in the shallowest zone which was dominated by small (<5 mm) mussels comprising 87% of dreissenids. An additional confounding factor was the relatively poor quality of images collected in the shallowest zone, where only 4 of the total of 30 images analyzed were of a high quality, limiting the usage of BIS. The difference between BIS and Ponar estimates in lake-wide *Dreissena* densities became smaller when we excluded stations with images that resulted in counts of “low confidence” and even smaller when we used only stations with video images of a “high confidence” (99% all 107 stations used; 77% only high and medium confidence stations; 43% only high confidence stations used). This trend in estimations of *Dreissena* density along with the increase in the image quality suggests that underwater videography could be improved with the improvement of video systems.

We found that if mussels <5 mm are excluded from Ponar estimates, the densities obtained with BIS and Ponar became almost identical (Table 2.2). The only significant difference was found in the shallowest, most turbid zone. The difference in the lake-wide estimates was within 10%. The mussels of very small size (<5 mm) contribute only a small proportion of total *Dreissena* population biomass, and their ecosystem impact is also limited. The large agreement in population estimates of mussels >5 mm between BIS and Ponar confirm that underwater videography is a very useful tool in *Dreissena* rapid population assessment. The next Lake Michigan CSMI survey will provide us with an opportunity to directly compare the 2021 and 2025 BIS datasets for changes in *Dreissena* population density estimated by rapid assessment.

Table 2.2. *Dreissena r. bugensis* density (mussels per m⁻², average ± standard error) and sample size (in parenthesis) in four depth zones and lake-wide averages estimated using Ponar grab and BIS in Lake Michigan in 2021. Only 107 stations for which both Ponar and BIS data were available were used in the table. Bold font indicates significant differences (P < 0.05) in paired t-tests.

Depth zone	BIS density	Ponar density, all mussels	Ratio between Ponar (all mussels) and BIS	Ponar density, mussels >5mm	Ratio between Ponar (mussels >5 mm) and BIS	Proportion of mussels > 5 mm, %
0-30 (19)	259±103	7365±4086	28.4	961±376	3.7	13
>30-50 (28)	3700±622	7864±1353	2.1	4514±518	1.2	57
>50-90 (38)	4969±330	6676±471	1.3	4989±418	1.0	75
>90 (22)	2581±596	4181±648	1.6	2318±499	0.9	55
Lake-wide (107)	3310±283	6596±828	2.0	3600±278	1.1	55

We also found an overall strong correlation between density estimation at the station level using BIS and Ponar (Fig. 2.1). The correlation coefficient ($R^2 = 0.81$) was high considering that *Dreissena* generally has a patchy distribution, as indicated by the fact that differences among replicates within a station can reach an order of magnitude or more. This high correlation between Ponar and BIS estimates is another confirmation that underwater videography is a reliable tool for surveying mussel populations.

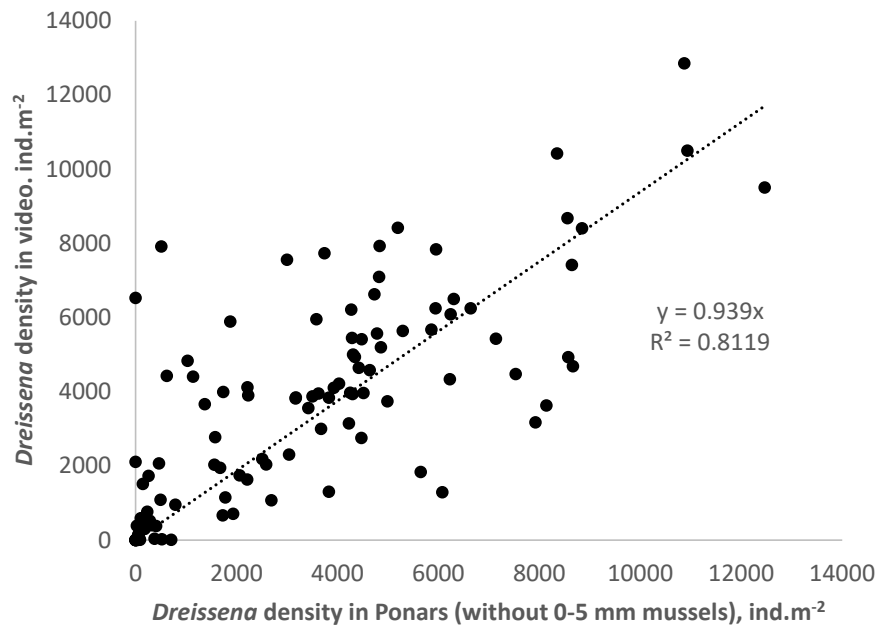


Figure 2.1. Relationship between *Dreissena* estimation using the BIS and Ponar (without mussels <5 mm) in Lake Michigan in 2021. The regression through the origin was significant (P < 0.001).

Acknowledgements

This study was funded by US EPA through the Great Lakes Restoration Initiative under Prime Agreement with Cornell University, Department of Natural Resources Award GL00E02254 “Great Lakes Long-Term Biological Monitoring 2017-2022” (PI Lars Rudstam) and Subaward # 82839-10916 to SUNY Buffalo State and supports the 2019 Lake Erie Cooperative Science and Monitoring Initiative. We appreciate the assistance of the captain and crew of the US EPA R/V *Lake Guardian* in sample collection. We thank Great Lakes Center research scientists Susan E. Daniel and Allison Hrycik, technicians Kit Hastings, Erik M. Hartnett, Brianne Tulumello and Angela Tulumello, and student technicians for help with sample processing. We are very grateful to Knut Mehler for preparing maps of *Dreissena* and *Diporeia* distribution, and to Annie Scofield, Elizabeth K. Hinchey (U.S. EPA GLNPO), and Susan Daniel for reviewing this report. We also would like to thank SUNY Buffalo State, Great Lakes Center Administrative Assistant Susan Dickinson for proofreading the report. Any views expressed in this report are those of the authors and do not necessarily represent the views or policies of the US EPA. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US EPA.

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Appendix. List of sampling stations.

Table A1. The 99 CSMI stations sampled on Lake Michigan in July 2021 and 15 long-term monitoring stations with information on lake basins, location (decimal coordinates), water depth, taxa reported, and main substrates. We used a coefficient of 19.12 to calculate density per m² for Ponar with a sampling area 0.0523 m². Taxa reported: All – all benthic taxa; D – *Dreissena* and *Diporeia* only. Samples from stations 9577 and MAN-2 (highlighted in grey) were not collected in July due to bad weather. Station 9577 was re-sampled during summer survey on September 6, 2021. Fifteen long-term monitoring stations sampled in September 2021 are listed below. In total, 342 samples from 114 stations were successfully collected from Lake Michigan in 2021.

Station	Basin	Latitude	Longitude	Depth, m	Sample type	Substrate
9552	Central	43.185	-87.2097	84.5	All	silty sand
9554	Central	43.2377	-86.8862	110	All	silt
9556	Central	43.3056	-87.7718	72	All	silty sand
9561	Central	43.4709	-86.7841	138	All	silt
9564	Central	43.6006	-87.3405	134.4	All	clay
9570	Central	43.8862	-86.9082	166	All	silt
9574	Central	44.0684	-87.1472	140	All	clay
9576	Central	44.1514	-86.6213	164.3	All	silt
9577	Central	44.2434	-87.3743	76	All	N/A
9582	Central	44.4084	-86.3684	121	All	silt and organic matter
9587	Central	44.6214	-86.3527	196	All	silt
9597	North	44.972	-86.3699	161.1	All	silt
74880	North	45.9085	-85.0249	24.9	All	sand and <i>Cladophora</i>
74900	North	45.4455	-85.2217	56	All	clay
76442	North	46.0009	-85.4095	19.6	D	silt and sand
76462	North	45.5348	-85.6359	57	All	silty sand
76471	North	45.2417	-85.5557	26.2	All	sand and shells
76482	North	45.0688	-85.8571	28.3	All	sand, silt, and shells
78030	North	45.8118	-85.7177	35	All	silt and sand
79612	North	45.9001	-86.105	20.1	All	sand
81220	North	45.7102	-86.4088	57.2	All	sand
81240	North	45.2474	-86.6692	56	All	sand
82851	North	45.05	-86.9227	81.2	All	silt, sand, and clay
82862	North	44.8576	-87.1896	12.7	All	sand
82882	Central	44.3893	-87.4226	60	D	sand
82902	Central	43.9182	-87.624	37.2	All	sand and clay
82922	Central	43.4469	-87.7961	18	All	sand and <i>Cladophora</i>

Station	Basin	Latitude	Longitude	Depth, m	Sample type	Substrate
84450	Green Bay	45.603	-87.0961	9.9	All	sand
95120	North	45.5235	-86.1695	135	All	silt
A-4	South	42.0582	-87.1085	73	All	silty clay
B-2	South	42.3999	-86.4507	50	All	silt
B-3	South	42.3996	-86.5914	62.5	All	silt
B-5	South	42.375	-87.3493	105	All	silt
B-6	South	42.3755	-87.4991	82.9	All	silt
B-7	South	42.3662	-87.666	47.5	All	clay and sand
C-1	South	42.8277	-86.2481	18	All	sand
C-2	South	42.8276	-86.3027	44	All	silt
C-3	South	42.8192	-86.4735	76	All	silt
C-45	South	42.1594	-87.5033	45.8	All	sand
C-5	South	42.8165	-86.8332	135	All	clay
C-6	South	42.7946	-87.4466	97.6	All	clay, sand, gravel
C-7	South	42.7921	-87.5747	50.8	All	sand
EG-12	South	42.3477	-87.6153	54.7	All	clay and sand
EG-14	South	42.3776	-86.7737	94.1	All	silt
EG-18	South	42.2936	-86.6431	58.6	All	silt
FR-1	Central	44.8166	-86.1397	21	All	sand and shells
FR-2	Central	44.8167	-86.1558	32	D	sand
FR-3	Central	44.8168	-86.1683	45	D	sand and silt
FR-4	Central	44.8165	-86.1852	56	All	sand and silt
FR-5	Central	44.8164	-86.1967	74.5	D	clay and sand
H-11	South	42.5542	-87.597	73.3	All	sand
H-15	South	42.1587	-87.4337	58.5	D	sand
H-18	South	41.983	-86.6006	18.6	All	sand
H-19	South	42.0001	-86.6848	35	D	silt
H-20	South	42.014	-86.7527	55	All	silt
H-21	South	42.0403	-86.8834	71	D	silt
H-24	South	42.3881	-86.3344	18	All	sand
H-31	South	43.0416	-86.3326	44	All	silt and sand
H-8	South	42.3993	-87.7711	13	All	clay, silt, and sand
H-9	South	42.4457	-87.7057	39.9	All	sand, shells, clay
K-2	Central	43.3371	-86.5004	48	D	sand and silt
L-220	Central	43.5008	-86.5032	21.2	D	sand
L-230	Central	43.5007	-86.5193	34.7	D	sand
L-245	Central	43.5008	-86.5316	43	All	sand, clay, and silt
L-260	Central	43.501	-86.5552	62	All	silt and woody debris

Station	Basin	Latitude	Longitude	Depth, m	Sample type	Substrate
L-280	Central	43.501	-86.6032	81.6	D	silt
M-45	South	43.1903	-86.4287	50	All	silt and sand
MAN-1	Central	44.4133	-86.2816	19.1	All	sand and shells
MAN-2	Central	44.413	-86.2853	36	D	N/A (not collected)
MAN-3	Central	44.4129	-86.3316	46.5	All	sand and clay
MAN-4	Central	44.4135	-86.3393	60.3	D	sand and clay
MAN-5	Central	44.4129	-86.3471	75.1	All	sand and clay
N-2	South	41.8917	-86.8668	37.4	All	silty clay
N-3	South	41.9665	-86.9833	60.8	All	silt
PET-2	North	45.4457	-85.0759	39.7	All	sand and clay
PW-2	Central	43.4471	-87.7819	30	All	silt
PW-3	Central	43.447	-87.7694	43	D	silt
PW-4	Central	43.4472	-87.7333	60.1	All	sand
PW-5	Central	43.4472	-87.6977	78.6	D	sand, clay, and silt
Q-13	South	42.8436	-87.7986	14.3	All	sand
Q-30	South	42.8431	-87.654	30.8	All	sand
S-2	South	41.7654	-87.3914	11.1	All	sand
S-3	South	41.8497	-87.3202	26	All	sand
S-4	South	41.9347	-87.2521	41.9	All	gravel
SB-2	North	44.8617	-87.1618	34.7	All	clay, silt, and sand
SB-3	North	44.8576	-87.1506	45	D	sand
SB-4	North	44.8571	-87.1366	60.7	D	sand
SB-5	North	44.8575	-87.0861	80.2	All	silty sand
SB-6	North	44.8575	-86.9232	157	All	clay and silt
SC-2	North	45.8412	-86.1054	31.2	D	sand
SC-3	North	45.8173	-86.1057	46	All	sand
SC-4	North	45.7899	-86.1053	65.9	D	silt
SC-5	North	45.7563	-86.1057	83	All	silt
SY-1	Central	43.9179	-87.6638	22	All	sand and shells
SY-4	Central	43.918	-87.5048	59.9	All	clay and sand
SY-5	Central	43.9184	-87.3756	79.1	All	silt
V-1	South	41.6966	-87.0133	17.8	All	sand
V-2	South	41.8165	-87.0484	29	All	sand
X-1	South	43.1376	-86.3615	36	All	silt and sand
X-2	South	43.2	-86.5171	105	All	silt and sand

Long-term monitoring stations:

Station	Basin	Latitude	Longitude	Depth, m	Sample type	Substrate
MI 11	South	42.38333	-87	128	All	silt
MI 18M	South	42.73333	-87	161	All	silt
MI 27M	Central	43.6	-86.9167	112	All	silt, sand
MI 30b	Central	43.93333	-86.5667	39	All	silt
MI 31b	Central	43.91667	-87.6167	42	All	fine silt
MI 40	North	44.76	-86.9667	160	All	silt
MI 41M	North	44.73667	-86.7217	250	All	silt
MI 42b	North	44.77056	-87.2128	49	All	sand, clay
MI 46b	South	43.10306	-86.3722	51	All	silt
MI 48b	South	42.68333	-86.3333	53	All	silt
MI 49b	Green Bay	45.49361	-87.0328	44	All	sand, silt
MI 50b	Green Bay	45.11667	-87.4167	20	All	silt
MI 51b	North	45.18333	-86.1	106	All	sand, silt, clay
MI 52b	North	45.80833	-86.0456	54	All	fine silt
MI 53b	North	45.43333	-85.2167	60	All	very fine silt